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METHODS, TOOLS, AND TECHNOLOGIES

A flexible tool to prioritize areas for conservation combining landscape units, measures of biodiversity, and threats

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Abstract. Expanding the reserve system is a key strategy to enhance biodiversity protection. Yet, conservation outcomes can be undermined by underrepresentation of some habitats and opportunistic placement of protected areas. Irreplaceability and vulnerability, the key principles of conservation, should thus be combined within a bioregionalization framework to implement protection in the habitats that most need it. We proposed a simple and flexible method to prioritize bioregions for conservation based on these principles and used it to rank the 85 bioregions of the Australian continent. To do so, we quantified biodiversity values and threats in each bioregion by gathering open-access data on species, landscapes, and land use. Bioregions were then ranked using a set of customizable scenarios, including ecologically meaningful combinations of measures of irreplaceability and vulnerability. To identify biodiverse areas under threat but potentially overlooked, we compared our results with the location of already established biodiversity hotspots (i.e., areas identified as important for biodiversity and under threat). We found that bioregions with the highest biodiversity values are predominantly located in the southwest, east, and north of the continent. Similarly, threats, particularly land clearance, are concentrated along the east coast and in the southwest. When ranking bioregions using scenarios including both threats and biodiversity values, the majority (75%) of the highest-ranking bioregions were already included in biodiversity hotspots. For five of these bioregions, the proportion of protected land to date still falls below the 17% recommended by the Convention on Biological Diversity and thus they likely require prompt prioritization and intervention. The method proposed can support ongoing monitoring and prioritization of land units for conservation. Its simplicity and flexibility mean it can be easily adopted for different areas and adjusted to local priorities.

Key words: Australia; bioregionalization; Interim Biogeographic Regionalization for Australia; invasive species; irreplaceability; land-use change; nature conservation; threatened species; vulnerability.

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Introduction

Regional threats to biodiversity, such as land-use change and invasive species, lead to range reduction, population decline, and increased extinction risk for many animal and plant taxa (Jetz et al. 2007, García-Valdés et al. 2015, Tilman et al. 2017). Land clearing causes habitat loss and degradation (Pimm and Raven 2000), while invasive species can act as new competitors, predators, or prey, and ultimately affect entire trophic cascades (Walsh et al. 2016). One of the main strategies to preserve biodiversity from these threats is the establishment of managed protected areas; as such, increasing their global coverage is one of the principal targets for 2020 as outlined at the Aichi Convention on Biological Diversity (CBD, Target 11). Yet, there is growing concern about the effectiveness of protected area networks, due to major geographic gaps at both global and local scales, and a distribution that fails to adequately reflect conservation priorities (Rodrigues et al. 2004*b*). For instance, in tropical areas, the savanna/grassland and deserts ecosystems are often neglected in favor of forest habitats (Bond and Parr 2010).

Globally, the identification of priority areas for conservation has been underpinned by the principles of conservation planning, based on the concepts of irreplaceability and vulnerability (Margules et al. 2002, Brooks et al. 2006). The term irreplaceability was originally used in ecological management to indicate how frequently a given site, among a group of hypothetical sites, is selected when evaluating alternative reserve system networks; sites selected more frequently are considered irreplaceable (Pressey et al. 1994). Recently, the term has become more broadly associated with the level of endemism of an area, particularly plant or bird species complemented by information on the number of other endemic vertebrates, as well as the rarity of habitat types in the region (Brooks et al. 2004, Mittermeier et al. 2011). Vulnerability describes the presence of threats (Gaston et al. 2002), such as land-use change and invasive species. For instance, Rodrigues et al. (2004*a*) adopted this approach to fill the gaps in the global protected area network by identifying regions where its expansion should be prioritized. The establishment of international biodiversity hotspots is another example of the application of these principles, with demarcation based on the proportion of plant and vertebrate endemism and the presence of threats (Myers et al. 2000).

Historically, protected areas have often been set aside opportunistically in locations unlikely to undergo major land transformations even without protection, such as impervious or low-productivity sites distantly located from roads and settlements, without consideration for threats or local biodiversity measures (Joppa and Pfaff 2009, Venter et al. 2017). Approaches have been developed to incorporate the principle of vulnerability (Gauthier et al. 2013) or both irreplaceability and vulnerability (Lawler et al. 2003, Reyers 2004, Tantipisanuh et al. 2016) at national or local scales, to better rank or identify sites based on a realistic assessment of conservation priority. In some instances, measures of irreplaceability and vulnerability have been calculated using ecologically meaningful minimal units of analyses, such as land units (Pressey and Taffs 2001, Noss et al. 2002, Overton et al. 2015). The concept of land units, defined as ecologically homogenous tracts characterized by similar biotic and abiotic attributes (Zonneveld 1989), is pivotal in landscape ecology, but has also been identified as valuable to natural resource management and conservation (Beier and Brost 2010), because it seeks explicitly to represent all ecological systems within the network of protected areas (Aycrigg et al. 2013). However, no technique has so far combined information on landscape- and species-based measures of biodiversity, threats, and land units within a simple, flexible, and integrated method that can be easily adjusted based on data availability.

Here, we propose just such an approach, to prioritize landscape units for biodiversity conservation based on open-access data, expanding on the concepts of irreplaceability and vulnerability. We used Australia as a case study because the country, with a wide climatic and biogeographic span, is among the top ten most biodiverse countries globally, already has a clearly defined biogeographic regionalization framework (Interim Biogeographic Regionalization for Australia [IBRA]), and has available a comprehensive biological open-access data inventory, as well as spatial data on historical land use and landscape biodiversity measures. We used the bioregional units within the IBRA framework (hereafter, "bioregion") to provide a novel and comprehensive land-unit-based overview of species- and landscape-based data on the irreplaceability and vulnerability. We then combined these characteristics in a suite of scenarios that sought to rank bioregions based on various importance weightings on biodiversity values, threats, or a combination. This enabled the inclusion of expert knowledge or local priorities in a quantitative framework; both are an important contributors to optimal conservation planning (Cowling et al. 2003). To locate potentially overlooked areas, we compared the distribution of the highest-ranking bioregions identified through our scenarios with that of already established biodiversity hotspots (national or international), which constitute areas already identified as important for biodiversity and under threat. To provide an illustration of the flexibility of this method, we also ranked bioregions based on ecological measures and threats for an exemplar taxon: amphibians. Our technique can thus be used to target both general biodiversity conservation and more specific conservation goals.

Methods

Study area

Australia is a megadiverse country that has experienced alarming rates of biodiversity loss, with 1318 plant and 448 animal species listed as threatened under the Environment Protection and Biodiversity Conservation (EPBC) Act (Jackson et al. 2017). Introduced species likely contributed most to mammal and reptile decline, leading to the extinction of 28 Australian native mammal species in the past 200 yr, the worst record for any continent in modern times (Johnson 2006). Land clearance has also been officially recognized as a key threat to biodiversity by the Australian Government since 2001 (Beeton et al. 2006), yet the country remains among those with the highest land-clearance rates globally (Waldron et al. 2017). To better devise natural protection plans, the IBRA framework was developed with the aim of representing ecological bioregions based on shared physical (climate, geology, and landforms) and biological (vegetation and species composition) characteristics (Thackway and Cresswell 1997). Originally, the implicit goal of IBRA was to achieve a spatially heterogenous protected network across the continent, via a quantitative target of at least 10% of land as protected within each bioregion; this target has recently been updated to 17%, in line with the recommendations from the Convention on Biological Diversity (Department of the Environment and Energy 2016). To date, this landscape unit has yet to be used to quantify vulnerability and irreplaceability metrics.

Spatial layers

Spatial information on land use in Australia came from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES). Land-use data were available for 1992, 1993, 1996, 1998, 2000, 2001, 2005, and 2010, at a spatial resolution of 0.01 decimal degrees (ABARES 2013). We classified as land clearance all land-use categories that met the Australian Threatened Species Scientific Committee definition established under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act): "destruction of the aboveground biomass of native vegetation and its substantial replacement by non-local species or human artefacts. [...] Land clearing includes clearance of native vegetation for crops, improved pasture, plantations, gardens, houses, mines, buildings, and roads. [...] It does not include silvicultural operations in native forests and manipulation of native vegetation composition and structure by grazing, burning, or other means." This left the following land-use categories: plantation forests, grazing modified pastures, cropping, perennial horticulture, seasonal horticulture, irrigated plantation forests, irrigated perennial or seasonal horticulture, and all intensive uses (intensive horticulture or animal production, residential, mining, manufacturing and industrial, services, utilities, and transport).

To assess the proportion of land subject exclusively to conservation, we included in nature conservation all land-use categories already listed under this type (Class 1.1) in the Australian Land Use Classification (ABARES 2016). This comprised the protected areas under the International Union for Conservation of Nature (IUCN) classes I to V and areas classified as other nature conservation. It excluded protected areas designated IUCN class VI, which are listed as managed resource protection designated primarily for the sustainable use of natural resources. Not all land-use categories fell under nature conservation or land clearance, with the sum of the two representing only land either being cleared or actively protected. Of the remaining areas, we classified as protectable (potentially available for nature conservation), land listed as public and included in the following land-use categories: managed resource protection, other minimal use, residual native cover, or grazing native vegetation.

Information on the most recent version of bioregion's names and borders (IBRA 7.0) was obtained from the Department of Sustainability, Environment, Water, Population and Communities (2013). Spatial layers outlining the extent of Australian threatened ecological communities, Ramsar wetlands (i.e., areas declared important for biodiversity at the Ramsar Convention on Wetlands of International Importance; Department of the Environment and Energy 2018), and Government's declared Important Wetlands in Australia were obtained from the Department of Environment and Energy. Spatial information on the distribution of chytridiomycosis (an amphibian fungal pathogen) in Australia was obtained combining data from Murray et al. (2010) and Ocock et al. (2013). Data on the geographic extent of international hotspots in Australia were provided by the Center for Applied Biodiversity Science at Conservation International (2011), and the extent of national biodiversity hotspots was extrapolated from the map on Australia's 15 National Biodiversity Hotspots (http://www.environment.gov.au); with the exception of the bioregion Coolgardie, the boundaries of biodiversity hotspots and bioregions overlap. Spatial data on the global key biodiversity areas (KBAs) were provided by BirdLife International (BirdLife International and Handbook of the Birds of the World 2017).

Species data

Data on Australian native and introduced species were obtained from the Atlas of Living Australia (ALA), which collects observations from a variety of sources, including scientific papers, citizen science projects, and museum collections (ALA: https://biocache.ala.org.au/). We gathered records for four taxonomic classes of vertebrates (Amphibia, Aves, Mammalia, and Reptilia) and two superclasses of plants (sensu Ruggiero et al. 2015), Angiospermae and Gymnospermae (for simplicity here called classes). We considered as invasive those plants listed as weeds in Randall (2007) and for animals, those species included in the list of exotic vertebrate animals in Australia (Vertebrate Pests Committee 2007). Records from before 1990 or missing spatial coordinates were excluded. This resulted in a collation of data on 26,580 species, of which 26,356 native: 23,573 plants and 2783 vertebrates (Data S1).

Land-use calculations were based on a subset of the native species meeting the following criteria:

1. Included in either the IUCN Red List (IUCN 2017) or the EPBC Act, to be able to associate the species to a threat code
2. Endemic to Australia, to ensure that the species' threat code is not a consequence of dynamics occurring outside the study area
3. More than 100 observations were available, for statistical robustness

For each endemic species selected, the threat code was recorded (LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; and CR, critically endangered), obtained from either the IUCN Red List or the EPBC Act. When a species was included in both lists, priority was given to the highest threat category. We adopted the IUCN terminology and considered a species to be threatened if classified as either VU, EN, or CR. The collated dataset included 23,831,959 observations on Australian endemic species: 36.2% were angiosperms, 0.1% gymnosperms, 0.8% amphibians, 56.9% birds, 4.9% mammals, and 0.9% reptiles. Among vertebrates, 127 amphibian species (of which 20 threatened), 173 mammals (41 threatened), 324 birds (25 threatened), and 209 reptiles (11 threatened) met the selection criteria. For plants, 290 angiosperm species (209 threatened) and 46 gymnosperms (9 threatened; Data S1) were selected.

Geospatial analyses

We used ArcMap v10.4 (ESRI, Redlands, California, USA) to calculate the metrics for all variables (by bioregion) used in the ranking process (Table 1), obtained by overlaying the species- and landscape-spatial data with the borders of the 85 mainland or continental-island bioregions across Australia (excluding Coral Sea, Indian Tropical Islands, Pacific Subtropical Islands, and Subantarctic Islands). Landscape parameters (e.g., land clearance, nature conservation, threatened species) were calculated as the proportion of the bioregion occupied by the metric of interest, while species metrics (e.g., native plants, weeds, invasive vertebrates) were calculated as the total number per bioregion. We then evaluated the changes in land clearance and nature conservation experienced by the selected endemic species. To remove the bias caused by multiple observations of one species recorded in the same location, the proportion of sites classified as land clearance or nature

Table 1. Species- and landscape-based metrics identified as descriptive of environmental values (irreplaceability and richness) and vulnerability (threats, decline, lack of assets).

Metric	Landscape	Species
Environmental values		
Irreplaceability	Number and extent of KBAs†	Number of native plants found in only 1 bioregion
		Number of native vertebrates found in only 1 bioregion
Richness	Number of vegetation communities	Number of native plants†
		Number of native vertebrates
Vulnerability		
Threats	Proportion of land clearance (2010)	Number of introduced weeds
	Proportion of land clearance change (from 1992 to 2010)	Number of introduced vertebrate pests
Decline	Extent of threatened ecological communities	Number of endemic threatened species‡
		Proportion of land clearance (across the country) of endemic threatened species‡ found in the bioregion
Assets (lack of)	Proportion of nature conservation (2010)	
	Proportion of protectable land (2010)	

† Key biodiversity areas.
‡ Those that met the criteria listed.

conservation was calculated for each endemic species by overlaying a grid of 1-km resolution on the Australian territory (excluded minor islands) and exporting only those grid cells where observations were present, regardless of the total number of observations per cell. Each grid cell was then associated with land-use data for all available years. The resultant datasets were exported as table and summaries in program R (R Core Team 2019) using the packages plyr (Wickham 2011) and dplyr (Wickham et al. 2017). Results are presented separately for each taxonomic class.

Metrics for bioregion ranking

For each bioregion, we calculated its landscape- and species-based measures of local environmental values (irreplaceability and richness) and vulnerability (threats, decline, lack of assets; Table 1). Irreplaceability parameters were used to describe the uniqueness of a bioregion, being the number of native plant and animal species found (within Australia) in only one bioregion, and the number and extent of KBAs as a landscape measure of irreplaceable areas crucial for biodiversity conservation (Eken et al. 2004). The number of native plant and vertebrate species and vegetation types found in each bioregion were used as a basic metric for species and habitat richness (Gotelli and Colwell 2001). Threats characterized habitat degradation and risks associated with invasive species: Proportion of land clearance and land-clearance change was used as a descriptor of landscape-based environmental threat, while the number of invasive species (weeds and vertebrate pests) represented species-based threats. Decline parameters addressed the environmental degradation already in place, based on the proportion of land occupied by threatened communities, the number of endemic threatened species found in the bioregion, and the proportion of land clearance they experienced across the country. Assets described land already (nature conservation) or potentially (protectable) available for conservation: Values were given a negative sign, so as the highest scoring bioregions were those with the least availability of land for conservation purposes. We did not include any metric for flexibility—defined as the replaceability of one location with another for conservation purposes (Margules et al. 2002)—because each bioregion represents a distinct landscape and thus cannot be considered replaceable. Parameter values for each bioregion are reported in Data S1.

Scenarios for priority ranking

Using the metrics summarized in Table 1, we defined 15 potential scenarios, representing ecologically meaningful combinations of parameters that could—depending on local data availability and ecological dynamics—be plausibly used to identify priority areas for conservation. Each metric in the scenario was assigned a relative weight, with a unity sum (Tables 2, 3). The first three scenarios emphasized the environmental values of a bioregion and include measures of species and habitat irreplaceability and richness. Scenario 1, based on the concept of irreplaceability, aimed to replicate (on a land-unit scale) the methods used to identify international biodiversity hotspots (Myers et al. 2000), giving more weight to the number of native plant species found in only one bioregion, but also accounting for the presence of native vertebrates not observed anywhere else in Australia. Unlike biodiversity hotspots, however, we also included the number of KBAs, as well as the proportion of land they occupied, as parameters. The second scenario addressed the concept of "richness" by using the number of native plant and vertebrates, as well as the number of vegetation types, while the third scenario included a combination of irreplaceability and richness measures. Scenarios 4–7, included in the macro-category vulnerability, targeted bioregions characterized by high levels of threat, based on land clearance and invasive species (scenario 4) or only land clearance (scenario 7), a low proportion of land considered an asset (nature conservation or protectable land; scenario 6), an emphasis on biodiversity decline (scenario 5), or a combination of threats and decline (scenario 8). The remaining scenarios, classified under mix, included different

Table 2. List of potential combinations (scenarios) of landscape parameters that can be used to determine priority areas for conservation.

	Weights—Landscape parameters							
Scenarios	Land clearance (%)	Land clearance change (%)	Nature conservation (%)	Protectable (%)	Land KBA (%)	No. of KBAs	No. of natural vegetation types	Land threatened communities (%)
Environmental values								
(1) Irreplaceability					0.1	0.1		
(2) Richness							0.2	
(3) Richness and irreplaceability					0.1	0.1	0.2	
Vulnerability								
(4) Threats	0.3	0.2						
(5) Decline								0.5
(6) Assets			0.6	0.4				
(7) Land use	0.3	0.3	0.2	0.2				
(8) Decline and threats	0.2	0.1						0.2
Mix								
(9) Richness, irreplaceability, and decline					0.1	0.1	0.1	0.1
(10) Richness and threats	0.2	0.1					0.1	
(11) Irreplaceability and threats	0.15	0.05			0.1	0.1		
(12) Richness, irreplaceability, and land clearance	0.4				0.1	0.1	0.1	
(13) Richness, irreplaceability, and land clearance change		0.4			0.1	0.1	0.1	
(14) Richness, irreplaceability, and lack of assets			0.2	0.1	0.1	0.1	0.1	
(15) All factors	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625

Notes: KBA, key biodiversity area. To improve readability, empty cells represent zeroes. The sum of all weights (landscape and species) in each scenario equals 1.

Table 3. List of potential combinations (scenarios) of species parameters that can be used to determine priority areas for conservation.

Scenarios	Weights—Species parameters							
	No. of native plants	Native plants in one IBRA	No. of native vertebrates	Native vertebrates in one IBRA	Weeds	Vertebrate pests	No. of endemic threatened species	Average LC of endemic threatened species (%)
Environmental values								
(1) Irreplaceability		0.5		0.3				
(2) Richness	0.4		0.4					
(3) Richness and irreplaceability	0.15	0.15	0.15	0.15				
Vulnerability								
(4) Threats					0.2	0.3		
(5) Decline							0.25	0.25
(6) Assets								
(7) Land use								
(8) Decline and threats					0.1	0.1	0.15	0.15
Mix								
(9) Richness, irreplaceability, and decline	0.1	0.1	0.1	0.1			0.1	0.1
(10) Richness and threats	0.2		0.1		0.1	0.2		
(11) Irreplaceability and threats		0.2		0.2	0.15	0.05		
(12) Richness, irreplaceability, and land clearance	0.05	0.1	0.05	0.1				
(13) Richness, irreplaceability, and land clearance change	0.05	0.1	0.05	0.1				
(14) Richness, irreplaceability, and lack of assets	0.1	0.1	0.1	0.1				
(15) All factors	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625	0.0625

Notes: IBRA, Interim Biogeographic Regionalization for Australia; LC, least concern. To improve readability, empty cells represent zeroes. The sum of all weights (landscape and species) in each scenario equals 1.

combinations of environmental values and vulnerability parameters. Scenarios 9–11 combined irreplaceability and richness with threats or decline, while scenarios 12–14 focused on the environmental impact of land use, by including both irreplaceability and richness, as well as either land clearance, land-clearance change, or lack of assets. The final scenario included all factors, with weights distributed equally. These scenarios are not meant to be definitive, merely illustrative: Using the code provided in Data S2, it is possible to fully customize scenarios, parameters, and metric weights to suit local conditions and priorities.

Example case study: Amphibians

The most concerning threats to amphibians are the spread of chytridiomycosis, land clearance, and climate change (Hof et al. 2011). Unlike the third threat, which requires joint international effort, the first two can be mitigated via local conservation action. Chytridiomycosis, caused by the fungus *Batrachochytrium dendrobatidis*, is linked to the decline and possible extinction of several amphibian species across the world (Kilpatrick et al. 2010). Land clearance is believed to affect amphibians through habitat destruction and degradation, roadkill, the use of fertilizer in agricultural lands, and possibly as a synergy by facilitating the spread of chytridiomycosis (Fahrig et al. 1995, Hamer et al. 2004, Kilpatrick et al. 2010).

To rank bioregions based on a specific taxonomic class, we adapted the approach described above using amphibian-specific parameters. Species metrics were the number of native amphibian species found in only one IBRA (irreplaceability), the total number of amphibian species (richness), the number of endemic threatened amphibian species and proportion of land clearance (across the country) experienced by endemic threatened amphibian species found in the bioregion (decline), and the proportion of the bioregion where chytridiomycosis was positively identified (threats). Landscape parameters were the extent of important wetlands (irreplaceability), the proportion of land clearance (2010) and land-clearance change (1992–2010) in areas where amphibians were observed (threats), and the proportion of nature conservation (2010) and protectable land (2010; assets—lack thereof). We adapted the scenarios shown in Tables 2, 3 to these parameters (Appendix S1: Table S1, Data S3).

Statistical analyses

For ranking, we normalized the metric-by-bioregion raw values using z-scores, calculated as $(x - \mu)/\sigma$, where x is the value for one bioregion, μ is the mean, and σ is the standard deviation. For each bioregion, the overall z-score was calculated by multiplying the z-score of each metric by the weight assigned to it in the scenario of interest and summing across all parameters. This operation was repeated for each scenario, varying the metrics included and the weights assigned as described in Tables 2, 3. Bioregions were ranked based on their overall z-score, and those falling into the 95th percentile—considered to represent the highest priority for that specific scenario—were compared with the location of already existing biodiversity hotspots. The R code used to calculate z-scores and rank bioregions is given in Data S2.

Results

Environmental values (irreplaceability and richness)

Bioregions showed marked differences in the parameters used to quantify irreplaceability and richness. The highest number of native plants (average 83 ± 15) or vertebrate animals (average 5 ± 2) found in only one bioregion (and thus measure of irreplaceability) was predominantly located in the southwest, east, and north of the continent (Fig. 1b, c), while KBAs (average number = 5.3 ± 0.5; average land cover = 11.1% ± 1.8%) were concentrated in bioregions in the north, central-east, and east (Fig. 1a). Similar patterns were evident in measures of richness, with the east and southwest exhibiting the highest number of native plants (average 1268 ± 86), vertebrates (average 486 ± 18), and vegetation types (average 15.2 ± 0.5; Fig. 1d–f).

Vulnerability

Land clearing was higher and increased more over time in bioregions located in eastern Australia and, to a lesser extent, in the southwest (Fig. 2a). Average land clearance increased from 14.3% (±2.2%) in 1992 to 22.1% (±3.0%) in 2010, but exceeded +50% in 15 bioregions, also predominantly located in the southwest and east of the country (Fig. 2b). The same geographical areas were also subject to occupation by the highest number of invasive species, particularly vertebrate pests (Fig. 2c, d). Nature conservation accounted for, on average, 14.0% (±1.5%) of land in 2010, similar to the average extent of protectable areas (14.1% ± 1.8%). Unlike the other metrics, nature conservation was more evenly distributed across the country (Fig. 2e), with the most protectable lands found mostly in the center and southwest (Fig. 2f). Decline parameters followed a distribution similar to threats, with the proportion of bioregions classified as harboring a threatened community being higher in the east, southeast, and southwest (with the exception of Arnhem Plateau in the tropics; Fig. 2g); the number of endemic threatened species was also higher in the east and southeast (Fig. 2h).

Across the country threatened endemic Australian species experienced, on average, 31.9% (±1.5%) of land clearance in 2010 (Data S1), corresponding to an average increase of 10.7% since 1992. Notable differences were observed between taxonomic classes, with the proportion of nature conservation exceeding that of land clearance for gymnosperms, amphibians, birds, and mammals (Fig. 3b–e), whereas the opposite was true for angiosperms (Fig. 3a), and reptiles after 2005 (Fig. 3f). Similar trends were observed for threatened and nonthreatened species within the same class, except for angiosperms and reptiles, where nonthreatened species showed a much lower proportion of land clearance than of nature conservation, unlike threatened angiosperms and reptiles (Fig. 3a, f).

Priority ranking

There was strong concordance between our results and the location of already established

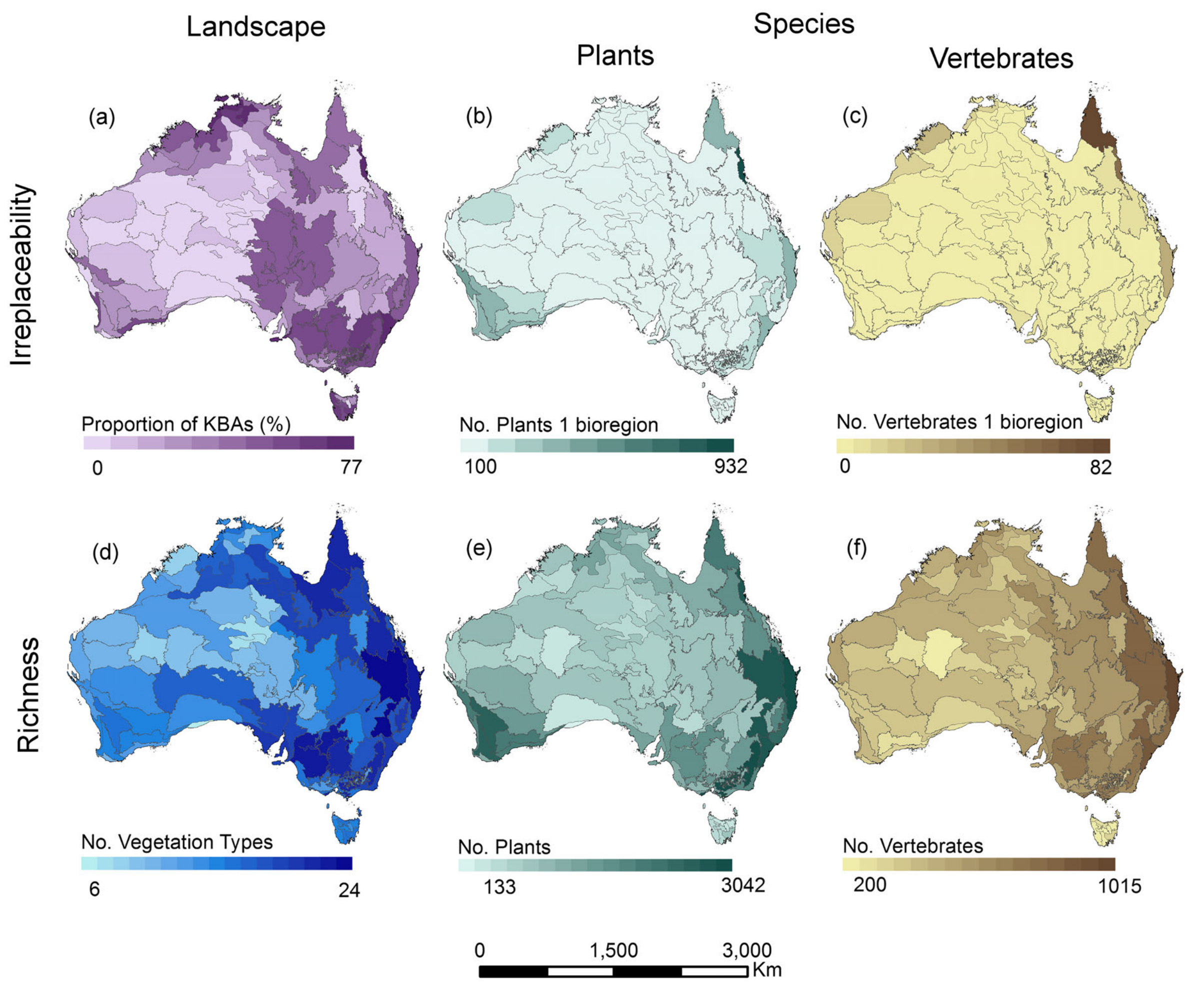

Fig. 1. Results, for each IBRA bioregion of Australia, of landscape and species metrics used to calculate measures of irreplaceability and biodiversity richness. Irreplaceability measures included (a) the proportion of a bioregion occupied by a KBA, and the number of (b) plants and (c) vertebrates found in only one bioregion. Richness measures were the number of (d) vegetation types, (e) plants, and (f) vertebrates found in each bioregion. The source shapefile is provided in Data S1.

biodiversity hotspots, despite being derived using different metrics, spatial units, and methodology. However, our approach identified additional bioregions and provided more fine-grained (and potentially flexible) breakdown of prioritization targets. For scenarios focused on environmental values (scenarios 1, 2, 3), the highest scoring bioregions (included in the 95th percentile) were predominantly located in already existing international or national hotspots, with the only exceptions being Cape York Peninsula and South Eastern Highlands (Table 4, Fig. 4a). For scenarios focused on either threats (scenario 4), decline (scenario 5), or land use (scenario 7), five of the 10 highest scoring bioregions were part of existing biodiversity hotspots (Tables 2, 3, Fig. 4b), although not any of the bioregions with the lowest proportion of nature conservation or protectable land (scenario 6, assets). The majority of bioregions included in mixed scenarios (combinations of biodiversity and vulnerability measures) were included in international (n = 5), or national (n = 3) biodiversity hotspots; the remaining bioregions were either located in the far north of the country (Cape York Peninsula) or in the

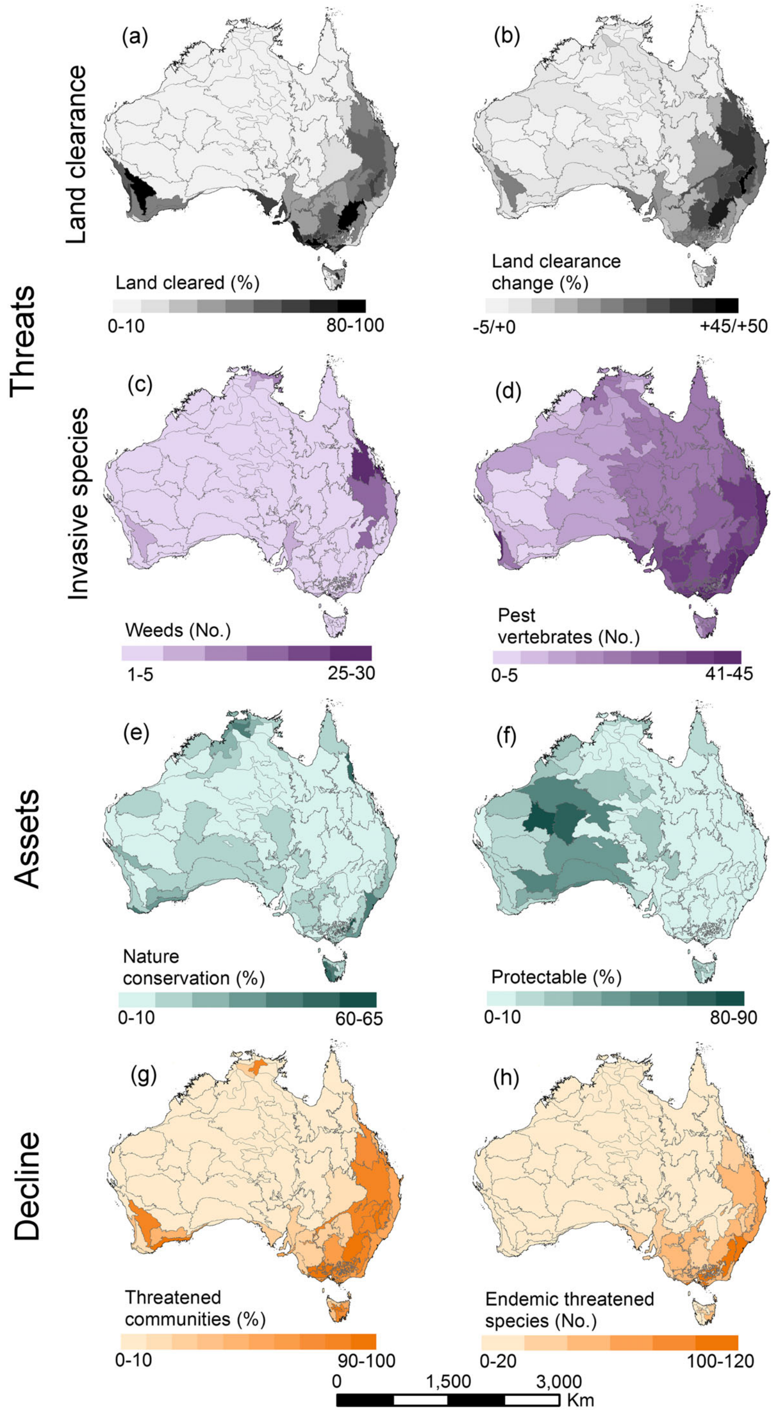

Fig. 2. Metrics used to assess vulnerability across bioregions. Threats included the proportion of (a) land clearance in 2010 and (b) land-clearance change from 1992 to 2010, as well as the number of (c) weed species and (d) vertebrate pest species. Assets included the proportion of (e) nature conservation and (f) protectable land in 2010, while decline parameters were (g) the proportion of land covered by threatened communities and (h) the number of Australian endemic threatened species found in the bioregion. The source shapefile is provided in Data S1.

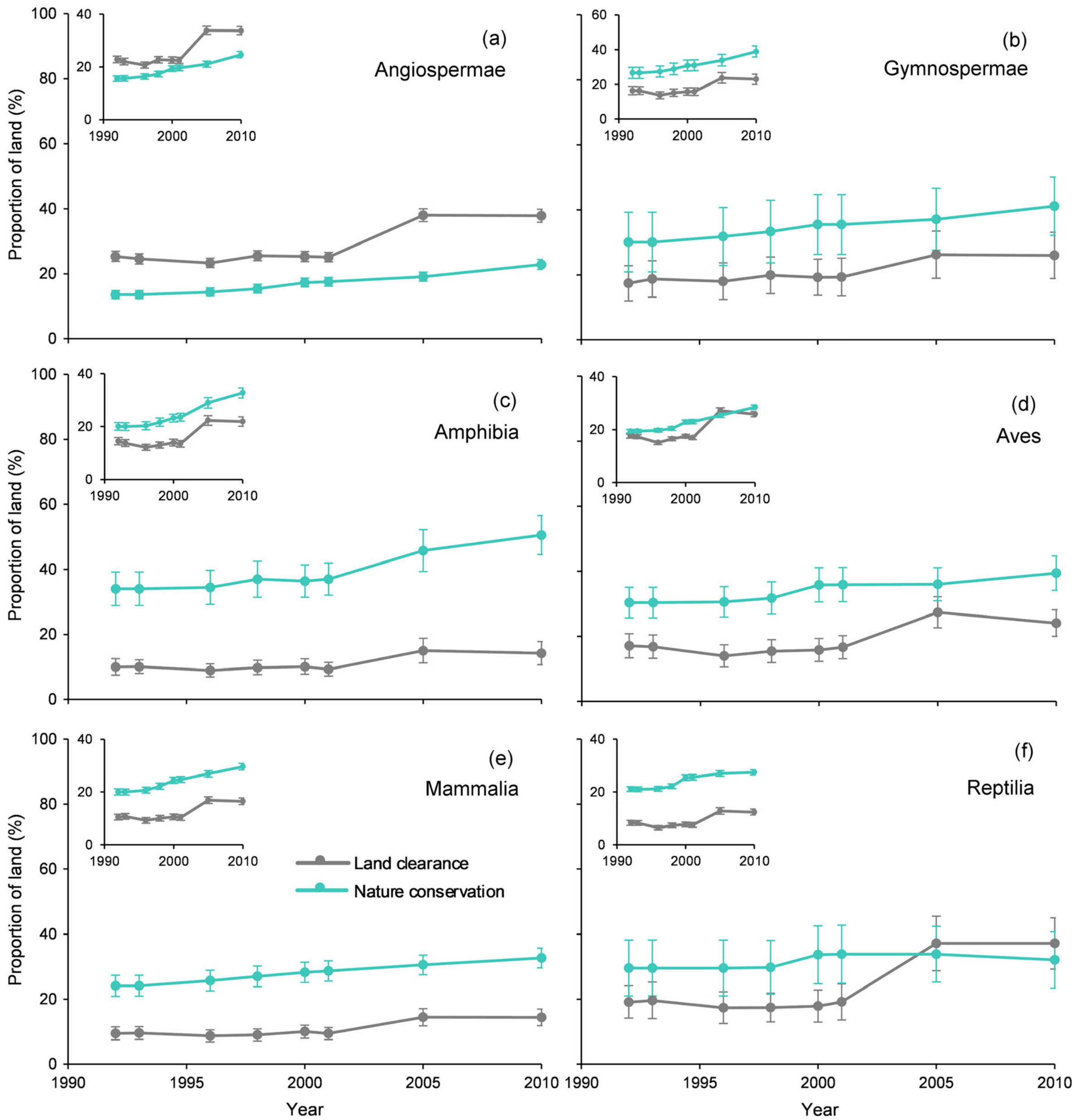

Fig. 3. Proportion of land where threatened species were broken down by its classification as either land clearance or nature conservation, over time. Results are reported as average for each taxonomic class: (a) Angiospermae, n = 209; (b) Gymnospermae, n = 9; (c) Amphibia, n = 21; (d) Aves, n = 25; (e) Mammalia, n = 41; and (f) Reptilia, n = 15. The insets show land-use trends for nonthreatened species (Angiospermae, n = 81; Gymnospermae, n = 37, Amphibia, n = 106, Aves, n = 299, Mammalia, n = 132, and Reptilia, n = 192). Error bars are standard errors.

southeast (NSW South Western Slopes, South East Coastal Plain, South Eastern Highlands; Fig. 4c). The full outcome of each scenario is reported in Data S1.

A similar pattern emerged for the amphibian case study, which highlighted the importance of the far northern and eastern portions of the country in terms of both environmental values

Table 4. Bioregions ranked in the 95th percentile of each scenario evaluated against the macro-categories of environmental values, threats and decline, and mix.

Scenarios	Bioregions Rank 1	Rank 2	Rank 3	Rank 4	Rank 5
Environmental values					
(1) Irreplaceability	Wet Tropics	**Cape York Peninsula**	South Eastern Queensland	Sydney Basin	Esperance Plains
(2) Richness	South Eastern Queensland	Brigalow Belt South	Sydney Basin	Wet Tropics	**South Eastern Highlands**
(3) Richness and irreplaceability	Wet Tropics	**Cape York Peninsula**	South Eastern Queensland	Sydney Basin	Brigalow Belt South
Vulnerability					
(4) Threats	**NSW South Western Slopes**	**South East Coastal Plain**	Brigalow Belt South	Southern Volcanic Plain	South Eastern Queensland
(5) Decline	**South Eastern Highlands**	Sydney Basin	Southern Volcanic Plain	**NSW South Western Slopes**	**Victorian Midlands**
(6) Assets	**Central Arnhem**	**Broken Hill Complex**	**Sturt Plateau**	**Mitchell Grass Downs**	**Darling Riverine Plains**
(7) Land use	**NSW South Western Slopes**	Nandewar	Brigalow Belt South	Southern Volcanic Plain	**Riverina**
(8) Decline and threats	**NSW South Western Slopes**	Southern Volcanic Plain	**South Eastern Highlands**	Brigalow Belt South	**South East Coastal Plain**
Mix					
(9) Richness, irreplaceability, and decline	Wet Tropics	Sydney Basin	South Eastern Queensland	**South Eastern Highlands**	**Cape York Peninsula**
(10) Richness and threats	South Eastern Queensland	Brigalow Belt South	**South Eastern Highlands**	Sydney Basin	**NSW South Western Slopes**
(11) Irreplaceability and threats	Wet Tropics	South Eastern Queensland	**NSW South Western Slopes**	**South Eastern Highlands**	Brigalow Belt South
(12) Richness, irreplaceability, and land clearance	Wet Tropics	South Eastern Queensland	**NSW South Western Slopes**	Kanmantoo	Avon Wheatbelt
(13) Richness, irreplaceability, and land clearance change	Wet Tropics	Brigalow Belt South	South Eastern Queensland	**NSW South Western Slopes**	Nandewar
(14) Richness, irreplaceability, and assets	Wet Tropics	**Cape York Peninsula**	South Eastern Queensland	Brigalow Belt South	Sydney Basin
(15) All factors	South Eastern Queensland	Sydney Basin	Brigalow Belt South	Wet Tropics	**South Eastern Highlands**

Note: Bioregions in bold are not included in any biodiversity hotspots.

and vulnerability, but also included a greater representation of tropical bioregions and part of the far-southern temperate forests of Tasmania, compared with the general biodiversity scenarios (Fig. 4d; Appendix S1: Fig. S1, Data S3). The tropical Gulf Plains, MacDonnell Ranges, Sturt Plateau, and Tiwi Cobourg ranked high when only threats were considered, despite the limited land clearance and the absence of chytridiomycosis, due to the lack of nature conservation or protectable areas, while the opposite was true for the bioregions in Tasmania.

Discussion

In Australia, biodiversity measures and threats varied markedly across bioregions. Our research was able to pinpoint bioregions of particular conservation value and, as importantly, show how weightings could be applied to metrics to landscape and species metrics so as to prioritize (or downplay) any given objective or goal. Under most scenarios, it was clear that bioregions with the highest values for irreplaceability or richness were predominantly located in the east and southwest of the country, and similar patterns

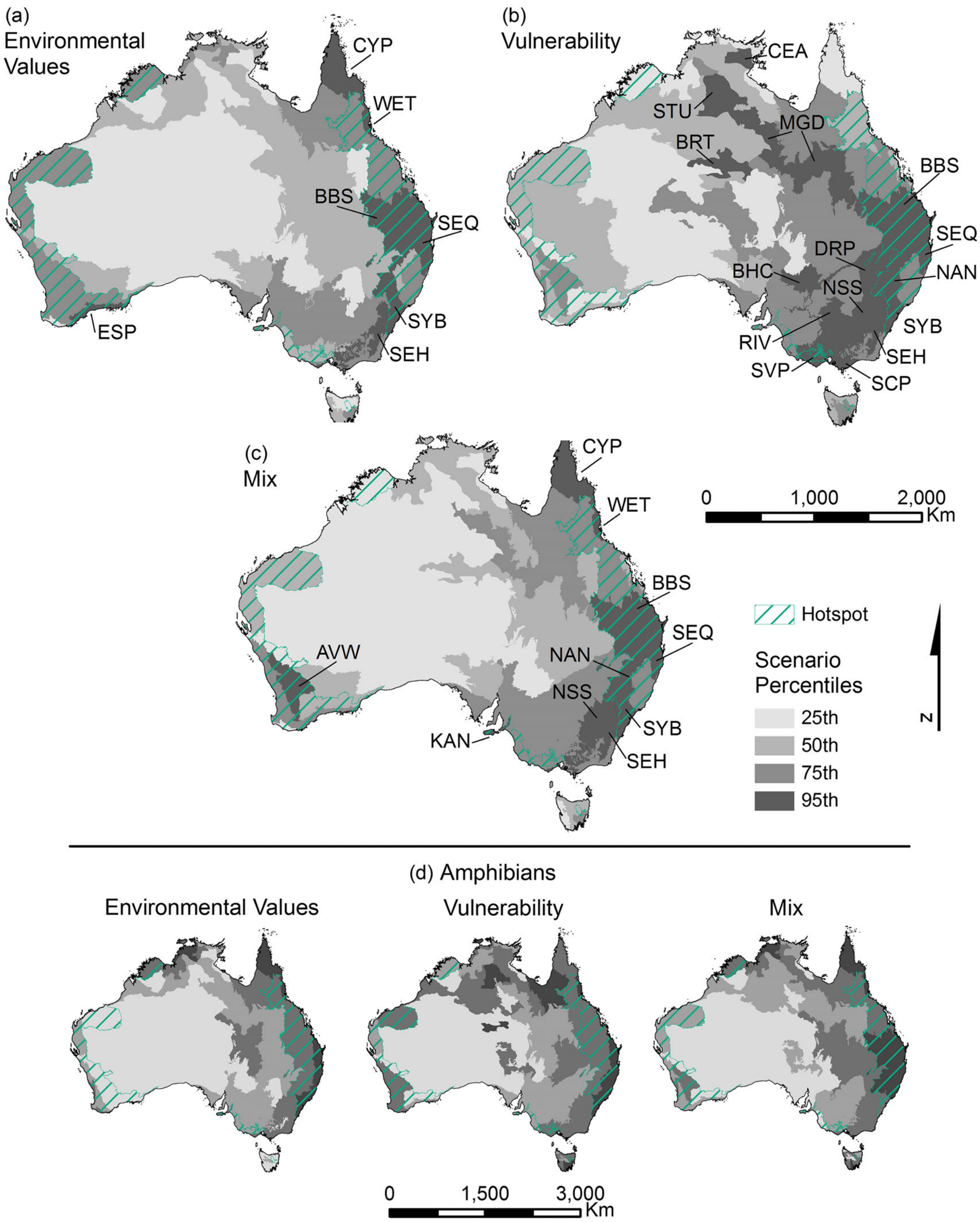

Fig. 4. Location of the highest scoring Australian bioregions for (a) scenarios focused on environmental values, (b) scenarios targeting threats and decline, and (c) scenarios including different combinations of the two. Bioregion codes are AVW, Avon Wheatbelt; BBS, Brigalow Belt South; CYP, Cape York Peninsula; ESP, Esperance Plains; KAN, Kanmantoo; NAN, Nandewar; NSS, NSW South Western Slopes; RIV, Riverina; SCP, South East Coastal Plain; SHE, South Eastern Highlands; SEQ, South Eastern Queensland; SVP, Southern Volcanic Plain; SYB, Sydney Basin; WET, Wet Tropics. The insets show the results for just the amphibian case study (for full-size amphibian maps, see Appendix S1: Fig. S1).

were also observed for vulnerability, particularly stemming from historical land clearance and its rate of change. This national-scale trend reflects a consistent phenomenon observed globally, whereby habitat conversion is exceeding nature conservation in most of the world ecoregions (Hoekstra et al. 2005). Australian endemic plant and animal species are also increasingly under pressure from land clearance across most bioregions, with threatened angiosperms and reptiles experiencing the highest increase in threat over time.

Through the quantification of ecological metrics and threats in all 85 mainland or continental-island bioregions across Australia, we identified landscapes at highest risk of degradation across all habitats, without implicitly assigning a higher value to forested areas, which could underestimate the threats to landscapes such as savannas, grasslands, and deserts (Bond and Parr 2010). The majority (75%) of the highest scoring bioregions (i.e., those falling into the 95th percentile) in the mixed scenario assessments (i.e., that included both threats and ecological measures) showed good concordance with the location of already existing national or international biodiversity hotspots (Table 4, Fig. 3). This suggests that the method proposed adequately represents the irreplaceability and vulnerability principles used to identify important areas for conservation. According to the latest data from the Collaborative Australian Protected Area Database (CAPAD; Department of the Environment and Energy 2016), 5 of the 10 highest scoring bioregions in the mixed scenarios currently reached an overall level of protection (including nature conservation and managed protected areas) above the 17% recommended by the Convention of Biological Diversity (Cape York Peninsula, Kanmantoo, South Eastern Highlands, Sydney Basin, and Wet Tropics). Of the remaining five, South Eastern Queensland achieved a proportion of protection of 14.1%, while in Avon Wheatbelt, Brigalow Belt South, Nandewar, and NSW South Western Slopes, the levels of protection still fall below 10%. Those under protected areas arguably require immediate prioritization and intervention.

The method we described and demonstrated in this paper explores the full potential of open-access ecological data, by linking these data to the institutional bioregional frameworks used to plan land management and conservation action (Theobald et al. 2000). While national platforms dedicated to storing biodiversity data, such as ALA, might not be present in every country, an increasing amount of species observations are lodged on international, open-access data repositories (e.g., the Global Biodiversity Information Facility [GBIF]), which represent an important source of information on species presence and distribution, yet are underused by planning agencies (Ondei et al. 2018). Further, data from citizen science projects, which harness the voluntary participation of non-trained observers to provide large volumes of ecological observations, can greatly enhance the geographic extent of professional scientific data, while also involving the public in the process of ecological monitoring (Theobald et al. 2015).

The use of species observational data might present some limitations. For instance, observations could underrepresent cryptic species or remote locations, or be biased toward more intensively studied taxa. Indeed, previous assessments on long-term open-access biodiversity data revealed a bias toward plants, birds, and amphibians (Theobald et al. 2015, Ondei et al. 2018), which was confirmed by our study, where bird and angiosperm records were in the majority. Species distribution models (SDMs), which predict species occurrence based on a chosen range of environmental parameters (Guisan and Thuiller 2005), are an alternative to observational records. However, SDMs can also be affected by sampling or modeling biases. However, such data can also be affected by sampling or modeling bias (Syfert et al. 2013, Guillera-Arroita et al. 2015) and are not always available for a wide range of species. In Australia, for instance, estimated species distribution data are supplied by the Department of Environment and Energy, but only for species of national environmental significance (https://www.environment.gov.au/science/erin/databases-maps/snes). CliMAS (http://climas.hpc.jcu.edu.au/) or Weed Futures (http://weedfutures.net/) also provide SDMs, but solely for animals or weeds, respectively. Species ranges can be downloaded from the IUCN spatial data portal (https://www.iucnredlist.org/resources/spatial-data-download); however, these data do not include plants, and since they were designed predominantly for global-scale analyses, they include a limited number of native species for each country and their resolution might not be appropriate for studies conducted at a national or more local scales (IUCN 2016). In our case study, the use of observation data provided an adequate representation of the biodiversity values of a bioregion, due to the large extent of our landscape units (i.e., bioregions), combined with the high number of observations stored in ALA, which were used to determine species presence (and by inference of sufficient sampling, absence). Nonetheless, more local applications of this method will need to account for these limitations and possibly include additional data (such as species range and density, and beta diversity) where available, at least for some focal species or communities (Noss et al. 2002).

Spatial layers, which were also entirely obtained from open-access sources, were also not exempt from caveats. For example, the latest comprehensive data on land clearance (covering all bioregions) end in 2010, but it is well established that, at least for some key bioregions, there has been substantial population growth in subsequent years (+10.4% from 2011 to 2018; Australian Bureau of Statistic, https://www.abs.gov.au/ausstats) alongside increases in agricultural production (Grundy et al. 2016). As such, there is an urgent need for more up-to-date information on land use. Further, while some were global in scope (e.g., KBAs) and could be used in any country, others were created at a national scale (e.g., land-use data, threatened vegetation communities); for those, global (lower-resolution) alternatives exist: for example, GlobeLand30 project (http://www.globallandcover.com) and Global Land Cover Share Database (http://www.fao.org). However, while some global spatial layers are easily accessible (such as in our case), they might not be as available, or accurate depending on the country or data of interest. For instance, while KBAs in Australia have been identified, mapped, and their level of threat assessed (BirdLife Australia 2017), other countries are still in the process of identifying their KBAs, particularly in marine habitats, and thus some important areas might still be missing (Donald et al. 2018). To prevent biases in the identification of priority areas for conservation, it is thus important to combine multiple data sources and evaluate the weight assigned to each one based on the known data accuracy.

To protect biodiversity and ecological processes, it is important to seek to preserve the entire landscape, rather than to focus on iconic species (Beier and Brost 2010). However, a focus on particular taxonomic units can be valuable to capture and ameliorate specific drivers of decline. In this context, we showed how our method can identify priority bioregions based on a distinct taxonomic target (amphibians) and found good agreement between the taxon-specific and general biodiversity assessments, albeit with some important differences: More tropical areas showed high levels of diversity and threats for amphibians, as well as two cool-temperate bioregions in southern-central Tasmania. While the latter seem to have been selected due to the greater spread of chytridiomycosis in cold-wet areas (Murray et al. 2010), for tropical areas this selection is overwhelmingly influenced by the high levels of amphibian species richness recorded in the tropical bioregions (Pyron and Wiens 2013).

In both ranking examples (Australian biodiversity generally, and amphibians specifically), the prioritization generated by a scenario-based solely on the lack of assets (nature conservation or readily protectable areas) included bioregions that did not rank high in any other scenario. A high proportion of these errant bioregions fall under the denomination of traditional indigenous uses (e.g., Central Arnhem = 98%, MacDonnell Ranges = 48%, and Tiwi Cobourg = 72%). While not officially listed under the category nature conservation, these areas are often managed for conservation by local Aboriginal groups, based on traditional ecological knowledge (Yibarbuk et al. 2001, Vigilante et al. 2017) and as such are not likely to be at high risk of being degraded by future anthropogenic development.

The severity of the impact of human land use on biodiversity and ecosystem services, as revealed by the bioregional metrics, underscores the need for effective measures to monitor its effects and prevent further habitat and species loss. These actions might include the expansion of the current protected area network (Aichi Target 11) as well as the implementation of tools and methodologies to “identify threats to biodiversity and determine priorities for conservation and sustainable use" (Aichi Target 19). However, approaches based on a single biodiversity level—be it species or ecosystems—cannot be relied upon in isolation to prioritize areas for conservation effectively, because conservation values embody a combination of these elements (Bonn and Gaston 2005, Brooks et al. 2006). Here, we have proposed a simple (yet powerful and flexible) method to link species observations with land-unit and national bioregionalization frameworks, by merging species- and landscape-based information on biodiversity and its threats and using weighted scenario analysis to rank land units (bioregions in our case study) and identify those in most need of protection. Once priority areas are identified, existing software which also accounts for connectivity (Ball et al. 2009, Moilanen et al. 2009) can be used to plan and implement reserve systems at the local-to-regional scale. Rather than relying on a fixed suite of metrics, our proposed approach (which can be run in the open-access software R) allows the user to choose and trade off various scenarios based on whatever priorities and data availability is most relevant or available to them. This feature, in combination with its ease of implementation and optional use of parameter weights, allows for incorporation of expert knowledge within a data-driven framework: an approach shown to improve the outcomes of conservation planning in a fast-changing world (Cowling et al. 2003).

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Literature Cited

ABARES (Australian Bureau of Agricultural and Resource Economics and Sciences). 2013. Land use of Australia, 1992–2010. Bioregional Assessment Source Dataset. http://data.bioregionalassessments.gov.au/dataset/98cea3eb-61a2-4e77-ad90-c280ec645c3a

ABARES. 2016. The Australian land use and management classification version 8. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra, Australian Capital Territory, Australia.

Aycrigg, J. L., A. Davidson, L. K. Svancara, K. J. Gergely, A. McKerrow, and J. M. Scott. 2013. Representation of ecological systems within the protected areas network of the continental United States. PLOS ONE 8:e54689.

Ball, I. R., H. P. Possingham, and M. Watts. 2009. Marxan and relatives: software for spatial conservation prioritisation. Pages 185–195 *in* A. Moilanen, K. A. Wilson, and H. P. Possingham, editors. Spatial conservation prioritisation: quantitative methods and computational tools. Oxford University Press, Oxford, UK.

Beeton, R., K. Buckley, G. J. Jones, M. Morgan, R. E. Reichelt, D. Trewin, and Australian State of the Environment Committee. 2006. Australia State of the Environment 2006. Independent report to the Australian Government Minister for the Environment and Heritage. 0642553009. Department of Environment and Heritage, Canberra, Australian Capital Territory, Australia.

Beier, P., and B. Brost. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. Conservation Biology 24:701–710.

BirdLife Australia. 2017. KBAs in danger: the state of Australia's key biodiversity areas in 2017. BirdLife Australia, Carlton, Victoria, Australia.

BirdLife International and Handbook of the Birds of the World. 2017. Bird species distribution maps of the world. Version 7. http://datazone.birdlife.org/species/requestdis

Bond, W. J., and C. L. Parr. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. Biological Conservation 143:2395–2404.

Bonn, A., and K. J. Gaston. 2005. Capturing biodiversity: selecting priority areas for conservation using different criteria. Biodiversity & Conservation 14:1083–1100.

Brooks, T. M., G. A. B. Da Fonseca, and A. S. L. Rodrigues. 2004. Protected areas and species. Conservation Biology 18:616–618.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Conservation Synthesis: Center for Applied Biodiversity Science at Conservation International. 2011. Biodiversity hotspots revisited, Conservation International, 2011. http://www.biodiversityhotspots.org/xp/Hotspots/resources/maps.xml

Cowling, R. M., R. L. Pressey, R. Sims-Castley, A. le Roux, E. Baard, C. J. Burgers, and G. Palmer. 2003. The expert or the algorithm? Comparison of priority conservation areas in the Cape Floristic Region identified by park managers and reserve selection software. Biological Conservation 112:147–167.

Department of Sustainability Environment Water Population and Communities. 2013. Interim Biogeographic Regionalisation for Australia (IBRA). Version 7 (Regions). Commonwealth of Australia 2017, Canberra, Australian Capital Territory, Australia.

Department of the Environment and Energy. 2016. Collaborative Australian Protected Areas Database (CAPAD). Commonwealth of Australia 2017, Canberra, Australian Capital Territory, Australia.

Department of the Environment and Energy. 2018. Ramsar list Wetlands of Australia. http://www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7BF49BFC55-4306-4185-85A9-A5F8CD2380CF%7D

Donald, P. F., et al. 2018. Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. Bird Conservation International 29: 177–198.

Eken, G., et al. 2004. Key biodiversity areas as site conservation targets. BioScience 54:1110–1118.

Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Taylor, and J. F. Wegner. 1995. Effect of road traffic on amphibian density. Biological Conservation 73:177–182.

García-Valdés, R., J.-C. Svenning, M. A. Zavala, D. W. Purves, and M. B. Araújo. 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. Journal of Applied Ecology 52:902–912.

Gaston, K. J., R. L. Pressey, and C. R. Margules. 2002. Persistence and vulnerability: retaining biodiversity in the landscape and in protected areas. Journal of Biosciences 27:361–384.

Gauthier, P., Y. Foulon, O. Jupille, and J. D. Thompson. 2013. Quantifying habitat vulnerability to assess species priorities for conservation management. Biological Conservation 158:321–325.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Grundy, M. J., B. A. Bryan, M. Nolan, M. Battaglia, S. Hatfield-Dodds, J. D. Connor, and B. A. Keating. 2016. Scenarios for Australian agricultural production and land use to 2050. Agricultural Systems 142:70–83.

Guillera-Arroita, G., J. J. Lahoz-Monfort, J. Elith, A. Gordon, H. Kujala, P. E. Lentini, M. A. McCarthy, R. Tingley, and B. A. Wintle. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24:276–292.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Hamer, A. J., J. A. Makings, S. J. Lane, and M. J. Mahony. 2004. Amphibian decline and fertilizers used on agricultural land in south-eastern Australia. Agriculture, Ecosystems & Environment 102:299–305.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Hof, C., M. B. Araújo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516–519.

IUCN. 2016. Guidelines for appropriate uses of IUCN RedList Data. https://www.iucnredlist.org/resources/guidelines-for-appropriate-uses-of-red-list-data

IUCN. 2017. The IUCN Red List of Threatened Species. Version 2017-3. http://www.iucnredlist.org

Jackson, W., et al. 2017. Australia state of the environment 2016: overview, independent report to the Australian Government Minister for the Environment and Energy. Australian Government Department of the Environment and Energy, Canberra, Australian Capital Territory, Australia.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology 5:e157.

Johnson, C. 2006. Australia's mammal extinctions: a 50,000-year history. Cambridge University Press, Port Melbourne, Victoria, Australia.

Joppa, L. N., and A. Pfaff. 2009. High and far: biases in the location of protected areas. PLOS ONE 4:e8273.

Kilpatrick, A. M., C. J. Briggs, and P. Daszak. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. Trends in Ecology & Evolution 25:109–118.

Lawler, J. J., D. White, and L. L. Master. 2003. Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. Ecological Applications 13:1762–1772.

Margules, C. R., R. L. Pressey, and P. H. Williams. 2002. Representing biodiversity: data and procedures for identifying priority areas for conservation. Journal of Biosciences 27:309–326.

Mittermeier, R. A., W. R. Turner, F. W. Larsen, T. M. Brooks, and C. Gascon. 2011. Global biodiversity conservation: the critical role of hotspots. Pages 3–22 *in* F. Zachos and J. Habel, editors. Biodiversity hotspots. Springer, Berlin, Germany.

Moilanen, A., H. Kujala, and J. Leathwick. 2009. The Zonation framework and software for conservation prioritization. Pages 196–210 *in* A. Moilanen, K. A. Wilson, and H. P. Possingham, editors. Spatial

conservation prioritization. Oxford University Press, Oxford, UK.
Murray, K., et al. 2010. The distribution and host range of the pandemic disease chytridiomycosis in Australia, spanning surveys from 1956–2007. Ecology 91:1557–1558.
Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.
Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone ecosystem. Conservation Biology 16:895–908.
Ocock, J. F., J. J. Rowley, T. D. Penman, T. S. Rayner, and R. T. Kingsford. 2013. Amphibian chytrid prevalence in an amphibian community in arid Australia. EcoHealth 10:77–81.
Ondei, S., B. W. Brook, and J. C. Buettel. 2018. Nature's untold stories: an overview on the availability and type of on-line data on long-term biodiversity monitoring. Biodiversity and Conservation 27:2971–2987.
Overton, J. M., S. Walker, R. Price, R. T. T. Stephens, S. Henson, R. Earl, and E. Wright. 2015. Vital sites and actions: an integrated framework for prioritizing conservation actions and reporting achievement. Diversity and Distributions 21:654–664.
Pimm, S. L., and P. Raven. 2000. Biodiversity: extinction by numbers. Nature 403:843–845.
Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. Biodiversity & Conservation 3:242–262.
Pressey, R. L., and K. H. Taffs. 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. Biological Conservation 100:355–376.
Pyron, R. A., and J. J. Wiens. 2013. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. Proceedings of the Royal Society B: Biological Sciences 280:20131622.
R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Randall, R. P. 2007. The introduced flora of Australia and its weed status. Cooperative Research Centre for Australian Weed Management, Adelaide, South Australia, Australia.
Reyers, B. 2004. Incorporating anthropogenic threats into evaluations of regional biodiversity and prioritisation of conservation areas in the Limpopo Province, South Africa. Biological Conservation 118:521–531.
Rodrigues, A. S. L., et al. 2004*a*. Global gap analysis: priority regions for expanding the global protected-area network. BioScience 54:1092–1100.
Rodrigues, A. S. L., et al. 2004*b*. Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643.
Ruggiero, M. A., D. P. Gordon, T. M. Orrell, N. Bailly, T. Bourgoin, R. C. Brusca, T. Cavalier-Smith, M. D. Guiry, and P. M. Kirk. 2015. A higher level classification of all living organisms. PLOS ONE 10: e0119248.
Syfert, M. M., M. J. Smith, and D. A. Coomes. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PLOS ONE 8: e55158.
Tantipisanuh, N., T. Savini, P. Cutter, and G. A. Gale. 2016. Biodiversity gap analysis of the protected area system of the Indo-Burma Hotspot and priorities for increasing biodiversity representation. Biological Conservation 195:203–213.
Thackway, R., and I. D. Cresswell. 1997. A bioregional framework for planning the national system of protected areas in Australia. Natural Areas Journal 17:241–247.
Theobald, D. M., N. T. Hobbs, T. Bearly, J. A. Zack, T. Shenk, and W. E. Riebsame. 2000. Incorporating biological information in local land-use decision making: designing a system for conservation planning. Landscape Ecology 15:35–45.
Theobald, E. J., et al. 2015. Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. Biological Conservation 181:236–244.
Tilman, D., M. Clark, D. R. Williams, K. Kimmel, S. Polasky, and C. Packer. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546:73–81.
Venter, O., A. Magrach, N. Outram, C. J. Klein, M. D. Marco, and J. E. Watson. 2017. Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. Conservation Biology 32:127–134.
Vertebrate Pests Committee. 2007. List of exotic vertebrate animals in Australia. https://www.pestsmart.org.au/list-of-exotic-vertebrate-animals-in-australia/
Vigilante, T., S. Ondei, C. Goonack, D. Williams, P. Young, and D. Bowman. 2017. Collaborative research on the ecology and management of the 'Wulo' monsoon rainforest in Wunambal Gaambera Country, North Kimberley, Australia. Land 6:68.

Waldron, A., D. C. Miller, D. Redding, A. Mooers, T. S. Kuhn, N. Nibbelink, J. T. Roberts, J. A. Tobias, and J. L. Gittleman. 2017. Reductions in global biodiversity loss predicted from conservation spending. Nature 551:364–367.

Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences USA 113:4081–4085.

Wickham, H. 2011. The split-apply-combine strategy for data analysis. Journal of Statistical Software 40:1–29.

Wickham, H., R. Francois, L. Henry, and K. Müller. 2017. dplyr: a grammar of data manipulation. R package version 0.8.3. https://CRAN.R-project.org/package=dplyr

Yibarbuk, D., P. J. Whitehead, J. Russell-Smith, D. Jackson, C. Godjuwa, A. Fisher, P. Cooke, D. Choquenot, and D. M. J. S. Bowman. 2001. Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. Journal of Biogeography 28:325–343.

Zonneveld, I. S. 1989. The land unit—a fundamental concept in landscape ecology, and its applications. Landscape Ecology 3:67–86.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2859/full